# THE TAXONOMY OF THE GENUS CAPSICUM (SOLANACEAE) - 1980[1]

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In 1977 it was suggested that any discussion of the taxonomy of the genus Capsicum should consider: 1) the generic limits of the several taxa in the subtribe Solaninae (Solanaceae), 2) the taxonomy of the wild species of Capsicum, 3) the taxonomy of the several domesticated species of Capsicum, and 4) how to treat the various cultivars and varieties now recognized within each domesticated taxon (Eshbaugh, 1977).

## 1. Generic Limits

The Solanaceous subtribe Solaninae established by von Wettstein in 1891, in Engler & Prantl's Die naturlichen Pflanzenfamilien, includes eleven genera of temperate-tropical distribution. They are Athenaea Sendtn., Bassovia Aubl., Brachistus Miers, Capsicum L., Chamaesaracha Gray. Melissea Hook., Nothocestrum Gray, Physalis L., Saracha Ruiz & Pav., Solanum L., and Withania Panq. Hunziker (1969a) recently reconstructed Witheringia L'Hert from various species scattered among several genera of the subtribes Solaninae and Lyciinae and it should be included in the Solaninae. Species of the genus Capsicum have been moved back and forth between no fewer than six genera in these two subtribes including Acnistus Schott., Athenaea, Brachistus, Bassovia, Withania, and Witheringia. Investigations using pollen morphology (Murry and Eshbaugh, 1971), gross morphology (Hunziker, 1950, 1960, 1961, 1967, 1969a, 1969b, 1971, 1977), epidermal morphology (Ahmad, 1963), etc., have served to clarify better the limits of each of these genera. Three especially comprehensive papers have recently appeared that have helped to clarify the taxonomy of the Solanaceae (D'Arcy, 1979; Hunziker, 1979a, 1979b). Nevertheless, several species of Capsicum continue to be included in quite different genera.

Morton (1938) suggested that Capsicum should be limited to plants with slender, free glabrous filaments, and a shiny, pungent berry. Heiser and Smith (1958) concurred in this viewpoint stating "we are convinced that those plants now placed in Capsicum which have soft, pulp-filled, non-pungent berries should be excluded from the genus." The presence of capsaisin, a volitile phenolic amine (Maga, 1975) may still be the best single diagnostic character for

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Table 1. Synopsis of the genus Capsicum based on recent additions and modifications (after Hunziker, 1956).

Tubocapsicum: C. anomalum

Pseudoacnistus: C. breviflorum

Capsicum

strictly wild species:

C. buforum *
C. campylopodium
C. chacoense
  var. tomentosum *
C. ciliatum
C. coccineum
C. cornutum
C. dimorphum
C. dusenii
C. galapagoensis
C. geminifolium
C. hookerianum
C. lanceolatum
C. leptopodum
C. minutiflorum
C. mirabile
C. parvifolium
C. scolnikianum *
C. schottianum
  var. flexuosum
C. tovari (?) *
C. villosum

domesticated species and spontaneous forms (hypothetical wild ancestors or weedy derivatives):

C. annuum
  var. aviculare * +
C. baccatum +
  var. pendulum*
    praetermissum * +
    tomentosum * +
C. cardenasii *
C. chinense *
C. eximium
  var. tomentosum *
C. frutescens
C. pubescens

* Taxa added since Hunziker's original treatment.

\+ Wild forms.

(?) C. tovari is not a validly published name at this time (see Heiser, 1976).

the genus. However, several species still included in the genus are not pungent, e.g. C. anomalum and C. ciliatum. Furthermore, the inheritance of pungency is controlled by a relatively simple genetic mechanism (Lippert et al., 1966) and wild non-pungent collections of many Capsicum species have been reported (I have several accessions of C. chacoense that exhibit this condition). Non-pungent forms are quite common among the several domesticated taxa.

The earlier descriptions of the genus Capsicum included taxa with rotate to subrotate corollas. Recent discoveries of campanulate corolla types in C. cardenasii (Heiser and Smith, 1958) and C. scolnikianum (Hunziker, 1961) require a modification of that concept. Both of these species may be unique among the peppers in being pseudo self-compatible.

Finally, most recent treatments of these several genera have seen Brachistus and Bassovia submerged into Witheringia. For example, Morton (1938) recognized thirteen species of Capsicum in Costa Rica including C. annuum and C. frutescens. Ten of these taxa have been reduced to six species of Witheringia by Hunziker (1969a). We are definitely closer to an understanding of generic limits in the Solaninae than we were fifteen or twenty years ago as witnessed by the recent treatments of these groups in several Latin American floras including the Flora of Panama (D'Arcy, 1973) and the Flora of Guatemala (Gentry and Standley, 1974).

## 2. Taxonomy of the Wild Species

von Wettstein (1891) divided Capsicum into two sections, Eucapsicum and the monotypic Tubocapsicum containing C. anomalum the only native (?) Old World species. Hunziker (1956) recognized three sections including the monotypic Tubocapsicum and Pseudoacnistus (C. breviflorum Sendt. confined to southeastern Brazil, southern Bolivia, Paraguay, and northern Argentina) and Capsicum which included twenty-four species. A re-analysis of Hunziker's synopsis of the genus Capsicum in light of discoveries during the past twenty years (Table 1) suggests that the section Capsicum should include twenty-two wild species and three varieties as well as five domesticated species and four varieties related to these taxa. Significant realignments of certain of these species can be anticipated as Brazilian material is better studied. There are new undescribed species which will also eventually be placed within the genus Capsicum. It is quite possible that some species currently recognized as belonging to the genus Capsicum will be removed from it after further investigation.

The importance of the wild species will be evident as their genetic material becomes more available to the plant breeder. It is essential that collections of these wild species be included in genetic banks and breeding programs throughout the world. However,

Table 2. Recent classifications of domesticated species of Capsicum and spontaneous forms (hypothetical wild ancestors or weedy derivatives).

| Heiser & Pickersgill (1969) | | D'Arcy & Eshbaugh (1974) |
|---|---|---|
| 1. C. pubescens Ruiz & Pavon | cultivated | C. pubescens |
| | spontaneous | C. cardenasii Heiser & Smith |
| | | C. eximium Hunziker |
| 2. C. baccatum var. pendulum (Willd.) Eshbaugh | cultivated | C. baccatum var. pendulum |
| C. baccatum L. var. baccatum | spontaneous | C. baccatum var. baccatum |
| 3. C. annuum L. var. annuum | cultivated | C. annuum var. annuum |
| C. annuum var. glabriusculum[1] (Dunal) Heiser & Pickersgill | spontaneous | C. annuum var. aviculare (Dierbach) D'Arcy & Eshbaugh |
| 4. C. frutescens L. | cultivated | C. frutescens |
| 5. C. chinense Jacq. | cultivated | C. chinense |

[1] Heiser & Pickersgill (1969) used C. annuum var. minimum (Miller) Heiser but have more recently used the above name Heiser & Pickersgill (1975).

the use of materials in this way will compound the taxonomic problem of dealing with the Capsicum species.

3. Taxonomy of the Domesticated Species

To appreciate fully the taxonomic problem of domesticated Capsicum one must return to the early literature. We know that Capsicum was discovered by Columbus on one of his first voyages to the New World (Anghiera, 1944) and that it was apparently introduced into the Old World at an early date in a variety of forms. The pre-Linnaean botanists described many different species and varieties of peppers. Fuchs (1542) recognized three taxa, Bauhin (1623) eight, Tournefort (1700) twenty-seven, and Miller (1754) eighteen. Linnaeus (1753) took a more conservative viewpoint in Species Plantarum describing just two species, C. annuum and C. frutescens. In his Mantissa (1767) he added two more species. Besser (1811) recognized seventeen taxa. Fingerhuth (1832) published the first true monograph of the genus, Monographia Generis Capsici, which included thirty-two species, seven of which were dubious and required further study, and twenty-eight varieties. The publication of Sendtner's (1846) analysis of Capsicum in the Flora Brasiliensis represented the first significant treatment of several valid wild species and domesticated taxa from a single geographic area. In 1852 Dunal published an extensive analysis of the genus in which he recognized fifty species with eleven more requiring further investigation. By the end of the nineteenth century more than ninety specific names had been associated with the genus Capsicum. In retrospect, much of the naming of Capsicum species was a result of taxonomists using primarily fruiting herbarium material to describe these taxa.

Irish (1898), at the urging of Stutevant and Rusby, published an extensive revision of the genus. He concluded that there were only two species including C. frutescens with one variety and C. annuum with seven varieties. Irish included C. pubescens as a species he was unable to examine. Bailey (1923) relegated the confusion of the preceding two hundred years to a single name, C. frutescens with five named varieties. Shinners (1956) took exception with Bailey's choice of name but was in agreement with his concept and accepted Kuntze's (1891) use of the single species C. annuum.

The treatments of the modern era, the past twenty-five years, are best summarized by Heiser and Pickersgill (1969) and D'Arcy and Eshbaugh (1974) (Table 2).

For those working with the evolution of domesticated Capsicum the obvious overlap of certain domesticated taxa has been a perplexing problem. Two recent approaches to the problem are illustrated by Pickersgill, Heiser, and McNeil (1979) using numerical analysis and Jensen, McLeod, Eshbaugh, and Guttman (1979) and McLeod, Eshbaugh, and Guttman (1979a, 1979b) using isoenzyme

analysis. These studies are in general agreement that C. pubescens and C. baccatum var. pendulum are clearly defined domesticated species. The question of the relationship of the C. annuum, C. frutescens, C. chinense domesticates is much more complex.

Pickersgill et al. see these three species as the end point of an evolutionary tree with very poor separation of these taxa in the semi-domesticated and ancestral wild forms. Thus at the lower end of the evolutionary scale it is numerically difficult to separate wild C. annuum and C. frutescens. Pickersgill et al. (1979) suggest that the ancestral gene pool of these domesticated taxa may have a single common karyotype.

Eshbaugh (1970) reports that intraspecific crosses between various collections (populations) of C. baccatum are accomplished at quite different levels of difficulty suggesting the genetic isolation of some of these collections. Pickersgill et al. say that within certain populations of C. annuum intraspecific crossing barriers are as or more pronounced than between C. chinense and C. frutescens. Pickersgill (1971) indicates that crosses between wild species of this three species complex are more likely to result in functional progeny than crosses between the different domesticated taxa of this complex. Eshbaugh (1975) concludes that although hybridization may be difficult and limited between three taxa it can be accomplished by several mechanisms including "genetic bridges" between the wild and domesticated taxa.

Jensen et al. (1979) using isoenzyme data and Nei's (1972) Standard Genetic Distance have shown that the distinction of C. annuum, C. frutescens, and C. chinense as species is somewhat arbitrary. In this analysis, alleles of several enzyme systems are used as taxonomic characters while each sample is treated as a separate OTU (Operational Taxonomic Unit). It can be shown that within each species many genotypes are repeated. When analyzing these species the OTU's were chosen to represent a given genotype at random. The final cluster analysis of these representative OTU's shows the complete dispersion of C. annuum, C. frutescens, and C. chinense genotypes amongst each other. The dendrogram and cluster analysis developed by this technique indicate that the three domesticates cannot be distinguished based on enzymatic profiles.

The unpublished data of Perrine (1980) using the kinetics of reassociation DNA indicate that C. annuum and C. frutescens are very closely related. In the three collections investigated Perrine has found that one collection of C. annuum is more closely associated and virtually indistinguishable from collections of wild C. chacoense. These data are in general agreement with portions of data from Pickersgill et al. and Jensen et al.

The dilemma is that two independent numerical analyses have suggested quite different conclusions. On the one hand Pickersgill

et al. find C. annuum, C. frutescens, and C. chinense as distinct based on morphology while Jensen et al. find the three taxa indistinguishable based on enzyme profiles. The problem posed by these two analyses is not unique to these investigators. It is in fact the basis for the taxonomic confusion within this complex over the past several hundred years. Pickersgill et al. state "it is easier to suggest the probable course of evolution in the C. annuum - C. chinense - C. frutescens group than to suggest a suitable taxonomic treatment."

Mayr (1970) and Grant (1971) have eloquently developed the concept of the taxonomic and biological species. The usefulness of these concepts has been debated by many authors (Sokal and Crovello, 1970). Nonetheless, when applied to the systematic problem of the domesticated chili peppers, some interesting anomalies arise.

If morphology is used as the primary basis for recognizing taxonomic species it is apparent that each of the five domesticated species can be maintained as a distinct category. The morphological separation of the spontaneous (wild) taxa is not nearly so clear. Capsicum eximium and C. cardenasii can be shown to intergrade morphologically within certain portions of their geographic range (Eshbaugh, unpublished) while they are distinct from C. pubescens. Wild C. baccatum is morphologically distinct from other wild species but intergrades into domesticated C. baccatum (Eshbaugh, 1970). Wild C. annuum, C. frutescens, and C. chinense morphologically fuse to form indistinguishable phenotypes at the most primitive level. Furthermore, each of the wild types shows a series of transitional forms from the wild to the domesticated taxa. If taxonomic logic is followed the variety C. annuum var. glabriusculum or its equivalent should be maintained while two new varieties are designated to represent the wild ancestral C. frutescens and C. chinense.

If one turns to the biological species concept to solve this dilemma other difficulties arise. The biological species is defined by Mayr (1970) as "groups of interbreeding natural populations that are reproductively isolated from other such groups" while Grant (1971) states that "it is the reproductively isolated system of breeding populations." Using this approach one can recognize only three domesticated species. These would include C. pubescens with C. eximium and C. cardenasii as a self contained breeding unit; C. baccatum as another such unit; and C. annuum, C. frutescens, and C. chinense as another unit genetically linked together by a wild ancestral gene pool. The problem with this approach is that certain populations within each of these biological species are in fact isolated from each other. Pickersgill et al. indicate that there are sterility barriers within C. annuum, from population to population, that are more pronounced than barriers

between C. chinense and C. frutescens. The same can be said for intrapopulational barriers in C. pubescens and C. baccatum.

Although this discussion has not served to provide a solution to the predicament of how to taxonomically treat the domesticated Capsicums it may well explain part of the dilemma faced by the early taxonomists who did not recognize the difference between the taxonomic and biological species. When this is considered in light of the many varieties, cultivars, races, forms, etc., created by man the problem of developing a rational taxonomy for the plant breeder and horticulturist becomes enormous.

## 4. Taxonomic Treatment of Subspecific Categories

The taxonomy of subspecific categories in Capsicum presents some especially vexing difficulties. Within the wild species, several local geographical variants have been described as varieties and this seems appropriate with respect to the general use of this category.

The real difficulty is in treating the variation encountered within the domesticated taxa. The two categories most commonly used have been subspecies and variety. Although the subspecies was used extensively by Filov (Terpo, 1966) in his treatment of cultivated Capsicum it seems inappropriate since the use of this category has customarily implied a geographical constraint that is not demonstrated within the domesticated chili peppers. The term variety has been used in two quite different ways in the systematic treatment of domesticated Capscium. One use has been to designate the wild (progenitor or weedy) and domesticated taxa as species pairs while another use has been to circumscribe each single morphological variant (Terpo, 1966) within a domesticated taxon. Although the use of variety may be appropriate in the former situation its use in the latter case may be inappropriate since for many the term variety still has geographical connotations of a somewhat smaller or more local scale.

In an attempt to deal with these difficulties several authors have developed elaborate hierarchical systems that seem to compound the problem. Jirásek (1961, 1966) developed an elaborate system employing twelve categories. Terpo (1966) used four of these terms to describe variation in C. annuum. Zhukovsky (1967) proposed a hierarchy for cultivated taxa which included six categories. Jeffrey believed (1968) that the variation encountered within a domesticated taxon could be adequately described with four basic categories and four supplemental categories to be used only in specialized situations as necessary. Harlan and de Wet (1971) envisioned a system that divided the wild and cultivated races into two subspecies with the variation of the cultivated species adequately described by four categories.

In the past decade numerical methods have been used to categorize groups of Manioc (Rogers and Fleming, 1973) and races of Maize (Goodman and Bird, 1977) with some degree of success but this methodology has not yet been applied to Capsicum.

One of the difficulties in developing a subspecific taxonomy in the genus Capsicum relates to convergent evolution within the three to five domesticated species. Subspecific classification has been based entirely on fruit shape, position, color, etc., and these characters have been altered by man in essentially the same pattern within each of the domesticates. Therefore, when morphology of the fruit is used to classify subspecific variation we encounter the problem of the fruits of several species which have evolved along parallel lines being included under a single varietal name. The morphology of C. pubescens fruits is distinct enough that varieties within this group should not be confused with various forms of the other domesticated peppers. However, the parallel development in C. annuum, C. chinense, C. frutescens, and C. baccatum has and will inevitably lead to erroneous conclusions regarding subspecific classificaitons. Is there an adequate solution to this predicament so that at least the workers within this genus can communicate intelligently with each other? At the present time it does not seem so. We are still unable to define the domesticated taxa to everyone's satisfaction. At the subspecific level categories are at best confused. A system such as Harlan and de Wet's (1971) is very useful although the various categories should be modified so as not to require that the concept of subspecies be interfaced where geographical parameters cannot be meaningfully invoked. Numerical methods will remain difficult to use at the subspecific level because of the very close morphological correlation of fruit characters in several of the domesticated taxa. Therefore, for the present it would seem that the best approach available for the horticulturalist and geneticist would be the use of the category cultivar with the appropriate "fancy" or common name as outlined under the International Code of Nomenclature for Cultivated Plants - 1969. To further assure each of us that we are all referring to the same material a system of race or strain numbers might prove useful. Nonetheless, such a system will be adequate for only a small sample of the known variation of the domesticated species since the vast majority of the variant material from South America has not come to the attention of plant breeders and horticulturalists. If Capsicum were a crop of the same importance of Manioc or Maize a system of subspecific taxonomy would have come into general usage long before now.

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